APPENDIX

Records, all of which are specimens, of *Mirafra albicauda* and *M. pulpa* in Ethiopia.

Mirafra albicauda				
21 Mar 1912	1♂	Lake Abaya, SE	*c.* 6°05′N, 37°55′E	Friedmann 1937
22 Mar 1912	2♂♂	Lake Abaya, S	*c.* 6°01′N, 37°50′E	Friedmann 1937
24 Mar 1912	1♂	Black Lake Abaya	*c.* 5°59′N, 37°46′E	Friedmann 1937
20 Sep 1990	1o	Nechisar Plain	6°00′N, 37°47′E	Safford in press
Mirafra pulpa				
19 May 1912	1♂	Sagon (=Sagan) River	5°10′N, 37°37′E	Friedmann 1937

Notes:

(a) The first 4 localities are within a few kilometres of each other and are best regarded as being the same and within the bounds of the Nechisar Plain. There is confusion over localities in Friedmann (1937): in his detailed list of collecting localities he states he was at North or "Black" Lake Abaya on 17–22 March 1912 and at South or "White" L. Abaya on 24–26 March (p. 8). I assume that the Black Lake mentioned on 24 March in the details of specimens collected (p. 17 in Part 2) is an error for White Lake, for the expedition was moving south then. Thus: Black Lake Abaya = L. Margherita = present day L. Abaya, 6°20′N, 37°55′E; White Lake Abaya = L. Ruspoli = present day L. Chamo, 5°50′N, 37°40′E; Nechisar Plain is centred on 6°00′N, 37°47′E.

(b) Berlioz (1922) records a ♂ specimen of *M. cheniana chadensis* = *M. cantillans chadensis* in May 1902 at 820 m on the Plaine Netch-sar ("rive gauche de l'Omo"). This could be the same as Safford's locality, although this is at 1100 m, because the collector was in the L. Abaya area in May and did not arrive at the Omo until later. However, there may be an error of locality or date, and there are others in the paper, so that in addition to the need to confirm the identification of this specimen there is another element of doubt involved.

Parapatric species of birds

by Jürgen Haffer

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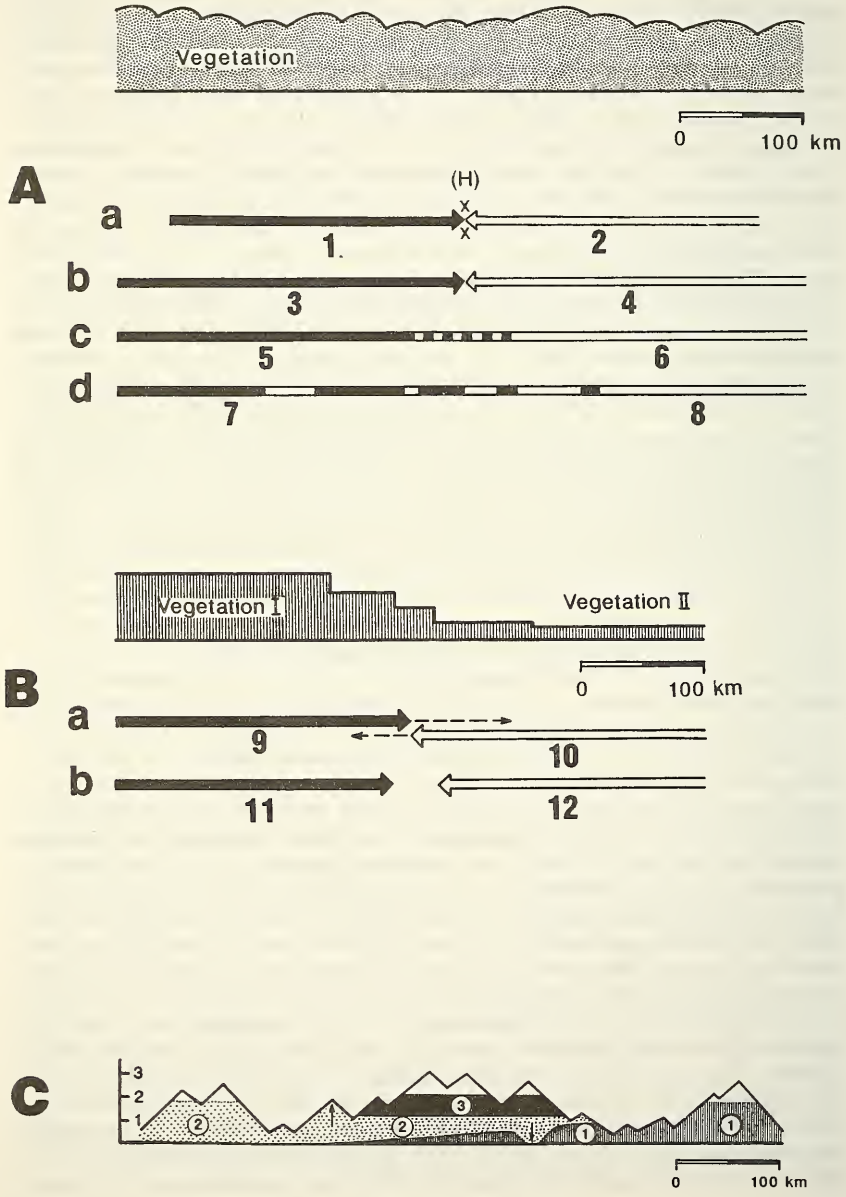
Parapatric species of birds occupy contiguous or narrowly overlapping ranges. They exclude each other geographically with no or only restricted hybridization along their contact zones, their abrupt replacement in many cases traceable over hundreds of kilometers. When hybridization occurs at the contact zone, the representatives are considered as species if each parental phenotype comprises at least 5% of the population along the contact zone (Short 1969, 1972). In these cases, the occurrence of parental phenotypes is indicative of impediments to gene flow. By contrast, a hybrid zone between subspecies consists exclusively or almost exclusively of variously intermediate individuals (hybrids), each parental phenotype comprising less than 5% of the population at the contact zone. Smith (1955, 1965) added 'parapatry' to the group of terms designating the geographical relationships of allied populations of organisms (allopatry, sympatry; see Mayr 1978). Parapatric species are more common than previously suspected, particularly in the tropics. Very few field studies

have so far tested the hypothesis that many parapatric distribution patterns are maintained by interspecific competition along the contact zones of the representative species.

Erwin Stresemann (1939: 360) discussed the geographical replacement of taxa which have reached genetic-reproductive isolation (and thus species status) but still retain the same ecological requirements. He stated: "Two (such) forms ... compete with each other for space and where they met during range extension, they abut sharply against each other without forming hybrids ... Examples of such situations are probably much more common than currently known" (translated from German). In a pioneering survey, David Lack (1944) investigated ecological aspects of the speciation process and recognized parapatry as one possible outcome of the interactions when differentiating forms come into secondary contact. One species is better adapted than the other in part of their combined ranges, the other in the rest, he said. Mayr (1951) and Vaurie (1955) stressed the theoretical importance of parapatric species listing, respectively, 18 and 23 "pseudo-conspecific" pairs from the Old World avifaunas. Keast (1961) and Vuilleumier (1981) discussed, from an ecological perspective, speciation phenomena in Australian and South American birds, respectively. General reviews of the ecological relationships of species including the occasional geographical exclusion of closely allied forms have been published by Mayr (1963, 1969), MacArthur (1972), Selander (1969, 1971), Brown & Gibson (1983), and Connor & Bowers (1987). Haffer (1989) reviewed the parapatric bird species of the Palaearctic Region.

Parapatry in animals involves the following three situations (Key 1981): First, *hybridization parapatry* between semispecies (*s. str.*) which form a "zone of overlap and hybridization" (Short 1969, 1972). In this case (Fig. 1, Aa) the two forms are genetically isolated despite the occurrence of (largely infertile) hybrids. Little backcrossing occurs. This situation grades into normal hybrid zones between subspecies. Among birds, no cases are known where, comparable to the morabine grasshoppers (Key 1981), post-mating isolating mechanisms have been fully developed prior to the functioning of pre-mating isolating mechanisms. In the grasshoppers mentioned above, individuals of the representatives hybridize freely at the contact zone but produce either no offspring or completely sterile young. Secondly, *competition parapatry* between paraspecies which exclude each other in an ecologically more or less uniform or gradually changing habitat zone with no or almost no overlap or hybridization about a sharply defined contact zone. The latter is often complex and intricate when studied in detail in the field (Fig. 1, Ab–d). The maintenance of the contact zone is here due to interactions between the species in contact (aggressive interference or resource exploitation). Thirdly, *ecological parapatry* comprises situations where an ecotone separates the ranges of two closely related or more distantly related bird species which inhabit, e.g., savanna on one hand and rain forest on the other hand. Geographical exclusion of these allies is an effect of totally different habitat preferences of the representatives and is not due to interspecific competition (Fig. 1, Bb). On the other hand, two representative species inhabiting adjoining and ecologically different vegetation zones which

merge gradually, e.g. regions of dry and moist forest zones, may exclude each other abruptly in the ecologically intermediate transition zone due to interspecific competition (Fig. 1, Ba). In such cases, the environmental



gradients do not seem to be steep enough to account for the abrupt geographic replacement of members of species pairs. In a similar manner, two more or less closely related allies of montane birds with comparable altitudinal preferences (as known from areas where only one of them occurs) may be segregated altitudinally due to ecological competition in areas where both occur (Fig. 1, C). In other cases, the altitudinal replacement of closely related species is due to their totally different ecological preferences, and interspecific competition is not implicated. We may generally distinguish between altitudinal or 'vertical' parapatry (and allopatry) and lowland or 'horizontal' parapatry (and allopatry). Probable examples for all situations listed above are known, although detailed field studies have been conducted in only a few selected cases. Large non-passerine birds may maintain parapatry even if they belong to very distinct species or genera; e.g. Ring-necked Pheasants exclude Prairie Chickens by monopolizing all the good cover (L.S. Short, pers. comm.). The term parapatry, as here understood, refers to the ecological relationships of vicariant species in contact irrespective of their systematic status as sister species or as less closely related species.

Numerous examples of parapatric species have been recognized in different groups of birds and other animals, particularly in the tropics, during recent decades (Mayr 1969, 1980, Mayr & O'Hara 1986, Hall & Moreau 1970, Snow 1978, Bock & Farrand 1980, Haffer 1974, 1986, 1987, 1989). The distribution patterns of superspecies resemble large-scale mosaics composed of the neatly interlocking ranges of the component semi- and paraspecies. The assumption that these species compete ecologically in some way or ways, and for this reason continue to replace each other geographically (Lack 1944, 1971, Mayr 1963, 1969, Selander 1971), has been tested by field studies in only a few cases. Very often, the basic pattern of geographic replacement probably is a legacy of the process of geographic speciation, whereas the mechanism of maintaining geographical exclusion along the contact zones presumably is a process of interspecific competition.

Figure 1. Ecological relations of parapatric species of birds. Schematic representation. A—Geographical replacement of species in a rather uniform vegetation zone. The range of each ally would be presumably more extensive in the absence of the respective geographical representative. (a) Hybridization parapatry between species 1 and 2; this situation grades into narrow zones of overlap and hybridization (and into broad overlap zones where occasional hybridization occurs). (b) Competition parapatry between species 3 and 4. (c) Overlap zone where species 5 and 6 remain interspecifically territorial. (d) Species 7 and 8 overlap their ranges to some extent occupying mutually exclusive patchy areas of varying size (these areas may or may not differ ecologically to some extent; e.g. higher *versus* lower terrain in a gently rolling landscape where the parapatric species meet). B—Geographical exclusion of species in the transition zone between ecologically different vegetation areas I and II (schematically indicated by a regionally changing environmental parameter). (a) Competition parapatry between species 9 and 10 whose ranges presumably would be somewhat more extensive in the absence of the competitor (dashed arrows). (b) Geographical replacement of species 11 and 12 which have totally different ecological preferences and are not in contact. C—Altitudinal species replacement in a mountainous region due to ecological competition. Species 1 and 2 have similar altitudinal ranges where they occur alone but segregate altitudinally where they come in contact. Species 2 ranges down to the lowlands and up into higher mountain zones where species 1 and 3, respectively, are missing (arrows). Vertical scale in thousand metres.

Terborgh (1971), Diamond (1973, 1975, 1986) and Terborgh & Weske (1975) reported abrupt replacements of related bird species along elevational gradients of tropical mountains which are probably due to ecological competition. Moreover, in the absence of several upper montane species on isolated mountain massifs the respective lower montane representatives expanded their elevational ranges correspondingly upward. Prigogine (1984a,b, 1985) summarized the available evidence for ecological competition between closely allied parapatric bird species in the African tropics emphasizing the dynamic nature of the contact zones, especially in mountainous regions. Short & Horne (1985) added information on interspecific territoriality in the barbets *Stactolaema whytii* and *S. anchietae* in the area of contact. In the north Temperate Zone, Short (1969) reviewed several species pairs which form zones of overlap and hybridization of varying width in North America (e.g. species of *Vermivora, Pheucticus, Passerina*) as well as closely related species which have only recently become broadly sympatric (species of *Sturnella*). Selander & Giller (1959, 1963), Emlen *et al.* (1975), Ferry & Deschaintre (1974), Ferry (1977, 1980), Faivre (1986), Martens (1982), Sorjonen (1986) and Lille & Moritz (1988), conducted field studies along contact zones of narrowly overlapping or completely parapatric species of woodpeckers, buntings, Old World warblers and nightingales, respectively, documenting competitive interactions and interspecific territoriality. Ferry (1977, 1980) identified sexual differences in species recognition as underlying reproductive isolation and interspecific territoriality in the warblers *Hippolais icterina* and *H. polyglotta*. Females of other species also use certain features of male songs and calls in species recognition whereas males do not (Searcy & Brenowitz 1988). Regarding some Old World warblers (e.g. species of *Sylvia, Acrocephalus, Locustella, Phylloscopus*), Cody (1979: 224) stated that close congeners with similar foraging ecologies may meet where their ranges abut or at intermediate points on a habitat gradient and defend territories between species as if but a single species were involved. This occurs particularly in simple or successional habitats.

The dynamic nature of the differentiation between geographically representative species is particularly obvious in those cases where the relations of sister species are different in different portions of the contact zone. Some selected examples are: *Milvus migrans* and *M. lineatus* hybridize at the contact zone in the Ural Mountains but are sympatric at a second area of contact in the western Himalaya (Stresemann 1959); *Buteo buteo* and *B. vulpinus* hybridize in the Mediterranean Region and broadly overlap in northeastern Europe (Glutz *et al.* 1971: 480); *Alectoris graeca* and *A. chukar* form hybrids in some areas of contact but not in others in eastern Bulgaria (Watson 1962, Dragoev 1974); *Larus argentatus* and *L. cachinnans* form hybrids at the Murman coast but do not hybridize at the coast of western France (Glutz & Bauer 1982; Yésou 1991); *Passer i. italiae* and *P. domesticus* hybridize along the contact zone in the Alps, whereas *P. i. hispaniolensis* and *P. domesticus* are broadly sympatric in an extensive overlap zone in the Mediterranean Region (Summers-Smith 1988); *Pipilo erythrophthalmus* and *P. ocai* hybridize in western and eastern Mexico but are sympatric without hybridization in other areas of the same region (Sibley & Sibley 1964).

The study of parapatric bird species along their contact zones has been largely neglected in the past, despite the preliminary analyses mentioned above and the availability of the detailed distribution maps of numerous superspecies of tropical birds published during the last 20 years (e.g. Hall & Moreau 1970, Snow 1978, 1982, Urban *et al.* 1986, Fry *et al.* 1988, Haffer 1974, 1987). Many of these maps graphically illustrate the exclusion patterns of paraspecies. However, it is not the systematist in the museum but, as B.P. Hall (in Hall & Moreau 1970: IX) emphasized, ". . . it is the man in the field . . . who can provide the key to many of the problems of relationship . . . and the maps draw attention to the critical areas in which comparative field study is most needed . . .", i.e. the areas of contact between parapatric species. "Such parapatric contact zones provide ecologists with a golden opportunity to discover the environmental factors that determine the placement of the dividing line at that particular location" (Mayr 1969: 14). Field studies are urgently needed in view of rapid habitat destruction by man in many areas of the world, particularly in the tropics.

Still to be determined for most instances of parapatry are:

(1) What is the situation regarding the local distribution of the representative species? Do the contact zones remain stationary or do they fluctuate regionally or shift gradually in a certain direction?

(2) In which manner is each zone of parapatry maintained? Which mechanisms assure reproductive isolation of the species along their zone of contact? Does reinforcement of pre-mating isolating mechanisms and/or of ecological segregation between the species take place at the contact zones? Do agonistic behavioural responses (interference competition) or resource preemption (exploitation competition) by their respective representatives prevent parapatric species from overlapping their ranges?

(3) Why did parapatry originate in each case? Are the locations of contact zones the results of historical causes or of current ecological conditions? Why do parapatric species not penetrate each other's ranges? In instances of sympatry, these species might be expected to maintain interspecific territories or to occupy mutually exclusive patchy areas of varying extent.

(4) When did the parapatric species originate and when did they establish contact?

These open problems of the ecological and systematic relationships of parapatric species need to be addressed regardless of whether some or all of the latter are considered taxonomically as species or still conspecific under a broad species concept. All cases of parapatry probably involve some level of reproductive interaction and reinforcement of pre-mating isolating mechanisms as well as of ecological segregation. Parapatric species illustrate the final stages of the speciation process which is complete only after sympatry of the two allies in contact has been achieved. However, not all speciating taxa pass necessarily through all stages of the microtaxonomic differentiation process (including the advanced stage of parapatry). Strongly isolated small populations on islands or on different continents may differentiate rather rapidly and directly from low levels of

microtaxonomic modification to the status of fully compatible biospecies. On the other hand, many continental species that differentiated through 'splitting' from fairly large isolated populations resulting from fragmentation of an ancestral continental species range, probably differentiated more slowly. Consequently, taxa at various intermediate levels of microtaxonomic differentiation are comparatively common in continental faunas (overlap and hybridization; parapatry). Emphasizing the importance of sexual selection and social competition during speciation in many groups of animals, West-Eberhard (1983) concluded that the maintenance of parapatric species boundaries may be due to competitive exclusion between populations which, in geographic separation, diverged rapidly and comparatively recently with respect to social characters (rather than ecological requirements). This interesting suggestion needs to be investigated in the numerous species pairs of birds with highly divergent life styles where parapatry occurs.

In order to direct the attention of field ornithologists to the relatively frequent occurrence of parapatry in birds and to facilitate the selection of species pairs for detailed study, I have compiled lists of examples of parapatric species from the Holarctic, Afrotropical, Neotropical and Australian avifaunas (Appendix). In most cases, these species are each other's closest relatives or at least are fairly closely related. On the basis of currently available information, they inhabit contiguous ranges excluding each other geographically with no or only restricted hybridization along their zones of contact. The latter are located in ecologically rather uniform habitats or in transition zones where, however, the often gradual ecological change does not explain the abrupt replacement of the representatives, one of which presumably is superior on one side of the contact zone, and the other species on the other side. Several contact zones probably follow more sharply defined ecotones. The lists in the Appendix are not complete. Additional parapatric species pairs certainly exist in regions which I have surveyed incompletely, like South America, and in other regions which I have not surveyed at all, like southeast Asia.

Some of the geographically representative species, upon close study of the contact zones, may be found to hybridize to such an extent that they have to be considered as conspecific. This, however, seems unlikely for most pairs listed since many specimens collected near the contact zones fail to show signs of hybridization. In several other cases, the representatives may turn out to be sympatric in a broad overlap zone where they may inhabit conspicuously different habitats, thus rarely coming in contact. In Amazonia, a number of parapatric representatives inhabit opposite sides of broad rivers which form the range limits at least over some distances. However, these representatives often are in direct parapatric contact in areas where the rivers cease to be barriers, either because they become increasingly narrow in the headwater regions or because one of the representatives has managed to cross the river barrier.

Ecologically similar representative species may develop or complete ecological segregation through competitive interactions in parapatry eventually permitting range overlap and sympatry, as suggested by Lack (1944), Mayr (1963), Bock (1979) and Grant (1986). However, the relatively frequent occurrence of parapatric species indicates that such

processes may take many thousands of years or more. The parapatric members of two musophagid species pairs in Africa are believed to have diverged from each other less than 1.4 and about 10 million years ago, respectively (Fry *et al.* 1988: XIII). In cases of three to six (or more) closely related parapatric or allopatric representative species which originated during several successive speciation events, the reasons for the delay in these species attaining ecological compatibility remain obscure.

Hopefully, field ornithologists will study increasingly the phenomenon of parapatry in birds to clarify the main open ecological and systematic problems associated with species which exclude each other geographically along sharply defined contact zones.

Summary

Parapatric species of birds occupy contiguous or narrowly overlapping ranges. They often exclude each other geographically along sharply defined contact zones. In ecologically fairly uniform or gradually changing regions, parapatric species either form a zone of overlap and hybridization (semispecies in *hybridization parapatry*) or they exclude each other without hybridization, probably due to ecological competition (paraspecies in *competition parapatry*). A third parapatric situation involves species inhabiting fairly distinct adjoining habitat zones where the species replace each other geographically along the ecotone (*ecological parapatry*). Only few parapatric contact zones of birds have been studied in sufficient detail to be certain about the cause of geographical replacement. Examples of apparently parapatric species in the Holarctic, Afrotropical, Neotropical and Australian avifaunas are listed in the Appendix to document the frequent occurrence of parapatry in birds and to encourage the study of these species in areas where they come in contact.

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APPENDIX

List of parapatric species of birds from the Palaearctic Region, North American Region, Afrotropical Region, Neotropical Region, and Australian Region.

Notes:

O—narrow overlap of ranges; H—limited hybridization at the contact zone; A—altitudinal replacement in regional contact zone.

Palaearctic Region: Examples as discussed by Haffer (1989).

North American Region: Examples are drawn from Mayr & Short (1970) and American Ornithologists' Union (1983) Check-list of North American birds, 6th edition.

Afrotropical Region: Examples are drawn from Hall & Moreau (1970), Snow (1978), Mayr & O'Hara (1986), Urban *et al.* (1986), Fry *et al.* (1988), Fry (1988). Numbers in front of many species names refer to the respective map number (P—passerine birds, Hall & Moreau 1970; NP—non-passerine birds, Snow 1978).

Neotropical Region: Numbers preceding species names refer to the following publications which include distribution maps and discussions: 1—Haffer 1967a, 2—Haffer 1967b, 3—Haffer 1969, 4—Haffer 1970, 5—Haffer 1974, 6—Haffer 1975, 7—Haffer 1977a, 8—Haffer 1977b, 9—Haffer 1985, 10—Haffer 1987, 11—Haffer 1988, 12—Delacour & Amadon 1973, 13—Snow 1982, 14—Novaes 1981, 15—Isler & Isler 1987.

Australian Region: Examples are drawn from Keast 1961, Blakers *et al.* 1984, and Ford 1987, his Fig. 5.

Palaearctic Region

Accipiter brevipes/*A. badius*/*A. soloensis*
Buteo rufinus/*B. hemilasius* (A)
Falco biarmicus/*F. cherrug*/*F jugger* (O)
Falco peregrinus/*F. pelegrinoides*
Alectoris rufa/*A graeca*/*A. chukar* (H)
Perdix perdix/*P. dauuricae*
Coturnix coturnix/*C. japonica*
Tragopan melanocephalus/*T. satyra*/*T. blythi*/*T. temminckii*
Lophophorus impeyanus/*L. sclateri*
Lophura leucomelana/*L. nycthemera* (H,A)
Lophura imperialis/*L. edwardsi*
Crossoptilon crossoptilon/*C. auritum*
Syrmaticus reevesi/*S. ellioti*
Chrysolophus pictus/*C. amherstiae*
Larus argentatus/*L. cachinnans* (H)
Streptopelia turtur/*S. orientalis* (O)
Merops apiaster/*M. leschenaulti*
Picus viridis/*P. squamatus*
Picoides leucopterus/*P. major*/*P. syriacus*/*P. assimilis*/*P himalayensis* (O,H,A)
Ammomanes phoenicurus/*A. cincturus*
Melanocorypha calandra/*M. bimaculata* (A)
Melanocorypha leucoptera/*M. mongolica*
Calandrella cinerea/*C. acutirostris*
Calandrella rufescens/*C. cheleensis*
Galerida cristata/*G. theklae* (A)
Alauda arvensis/*A. gulgula*
Eremophila alpestris/*E. bilopha* (A)
Ptyonoprogne fuligula/*P. rupestris*/*P. concolor*
Delichon urbica/*D. dasypus*
Anthus campestris/*A. godlewskii*
Anthus spinoletta/*A. rubescens*
Motacilla flavissima/*M. flava*/*M. lutea*/*M. taivana*
Motacilla alba/*M. maderaspatensis* (A)
Luscinia magarhynchos/*L. luscinia* (O)
Luscinia pectoralis/*L. calliope* (A)
Saxicola torquata/*S. leucura*
Oenanthe hispanica/*O. pleschanka* (H)
Oenanthe leucura/*O. leucopygia*
Turdus naumanni/*T. ruficollis* (H)
Turdus obscurus/*T. pallidus*
Locustella fluviatilis/*L. lanceolata*
Locusstella naevia/*L. certhiola*/*L. ochotensis* (H)
Acrocephalus arundinaceus/*A. stentoreus*
Hippolais polyglotta/*H. icterina* (O)
Hippolais olivetorum/*H. languida*
Sylvia curruca/*S. althaea*/*S. minula* (H,A)
Sylvia melanocephala/*S. mystacea*

Phylloscopus collybita/*P. lorenzii* (A)
Phylloscopus trochiloides/*P. nitidus*
Phylloscopus affinis/*P. subaffinis*
Ficedula albicollis/*F. semitorquata*
Garrulax maximus/*G. ocellatus* (A)
Pomatorhinus erythrogenys/
P. erythrocnemis
Paradoxornis paradoxa/*P. unicolor*
Aegithalos niveogularis/*A. iouschistos*
Aegithalos concinnus/*A. leucogenys*
Parus major/*P. bokharensis* (H)
Parus caeruleus/*P. cyanus* (H,O)
Parus rubidiventris/*P. beavani*
Parus xanthogenys/*P. spilonotus*
Sitta nagaensis/*S. castanea*
Lanius collurio/*L. cristatus*
Lanius tephronotus/*L. schach* (A)
Corvus monedula/*C. dauuricus* (H)
Corvus corone/*C. torquatus*
Corvus corax/*C. ruficollis* (H)
Sturnus unicolor/*S. vulgaris* (O)
Passer domesticus/*P. italiae*/*P. indicus* (H)
Pycnonotus leucotis/*P. leucogenys* (H)
Carduelis flammea/*C. hornemanni* (O)
Loxia curvirostra/*L. scotica*
Bucanetes githagineus/*B. mongolicus* (A)
Emberiza melanocephala/*E. bruniceps* (H)
Emberiza cia/*E. godlewskii*
Emberiza hortulana/*E. caesia*/
E. buchanani (A)

North American Region

Gavia immer/*G. adamsii* (H)
Gavia arctica/*G. pacifica* (H)
Plegadis falcinellus/*P. chihi* (O)
Callipepla californica/*C. gambelii* (H)
Pluvialis dominica/*P. fulva* (O)
Larus thayeri/*L. glaucoides*
Selasphorus rufus/*S. sasin*
Picoides scalaris/*P. nuttalli* (H)
Melanerpes carolinus/*M. aurifrons*/
M. uropygialis (H)
Sphyrapicus varius/*S. ruber* (H)
Contopus virens/*C. sordidulus* (H)
Parus hudsonicus/*P. cinctus*/
P. rufescens
Parus atricapillus/*P. carolinensis*
Dendroica occidentalis/*D. townsendi*
Pheucticus ludovicianus/
P. melanocephalus
Passerina cyanea/*P. amoena* (H,O)
Polioptila californica/*P. melanura*

Afrotropical Region

NP 79 *Circaetus cinerascens*/*C. fasciolatus*
NP 85 *Accipiter tachiro*/*A. toussenellii* (H)
NP 88 *Melierax metabates*/*M. canorus*/
M. poliopterus
NP 93 *Buteo augur*/*B. rufofuscus*
NP 117 *Falco ardosiacus*/*F. dickinsoni*
NP 122 *Francolinus ahantensis*/
F. squamatus
NP 124 *Francolinus leucoscepus*/
F. rufopictus/*F. afer*/
F. swainsonii
NP 125 *Francolinus bicalcaratus*/
F. clappertoni/*F. icterorhynchos*/
F. hildebrandti/*F. natalensis*
NP 128 *Francolinus albogularis*/*F. schlegelii*
NP 137 *Guttera edouardi*/*G. plumifera*/
G. pucherani
NP 166 *Eupodotis vigorsi*/*E. rueppellii*
NP 169 *Eupodotis afra*/*E. afraoides*
NP 170 *Neotis denhami*/*N. heuglini*
NP 171 *Neotis kori*/*N. arabs*
NP 180 *Vanellus spinosus*/*V. armatus*
NP 193 *Cursorius temminckii*/*C. cursor*
NP 215 *Streptopelia vinacea*/*S. capicola*
NP 225 *Turtur abyssinicus*/*T. chalcospilos*
NP 228 *Treron calva*/*T. waalia*
NP 229 *Poicephalus gulielmi*/*P. robustus*
NP 230 *Poicephalus meyeri*/*P. senegalus*/
P. crassus/*P. flavifrons*/
P. rufiventris/*P. cryptoxanthus*/
P. rueppellii
NP 232 *Agapornis pullaria*/*A. personata*
NP 235 *Crinifer piscator*/*C. zonurus*/
Criniferoides leucogaster
NP 236 *Corythaixoides personata*/
C. concolor
NP 237 *Tauraco persa*/*T. schutti*/
T. livingstonii/*T. fischeri*
NP 237 *Tauraco livingstonii*/*T. corythaix*
NP 239 *Musophaga violacea*/*M. rossae*
Musophaga johnstoni/
M. porphyreolophus
NP 253 *Centropus leucogaster*/*C. anselli*
Cercococcyx olivinus/
C. montanus (A)
Caprimulgus inornatus/*C. stellatus*
Caprimulgus climacurus/*C. clarus*/
C. fossi
NP 295 *Apus bradfieldi*/*A. barbatus*
NP 299 *Colius striatus*/*C. castanotus*
NP 300 *Urocolius macrourus*/*U. indicus*
NP 311 *Halcyon senegalensis*/
H. senegaloides
NP 315 *Merops bulocki*/*M. bullockoides*
Merops variegatus/
M. oreobates (A)
NP 325 *Coracias abyssinica*/*C. caudata*
Phoeniculus cyanomelas/
P. aterrimus
NP 335 *Ceratogymna fistulator*/
C. bucinator
NP 337 *Bucorvus abyssinicus*/*B. leadbeateri*
Tockus fasciatus/*T. alboterminalis*/
T. bradfieldi

NP 344 *Lybius dubius*/*L. rolleti*/*L. bidentatus*
NP 346 *Lybius leucocephalus*/*L. rubrifacies*/*L. torquatus*
NP 349 *Lybius frontatus*/*L. leucomelas* (H)
NP 352 *Stactolaema anchietae*/*S. whytii*/*S. leucotis*
NP 354 *Gymnobucco peli*/*G. sladeni*
NP 367 *Indicator conirostris*/*I. minor* (H)
NP 377 *Campethera punctuligera*/*C. nubica*/*C. bennettii*
NP 379 *Campethera maculosa*/*C. cailliautii*
NP 388 *Dendropicos pyrrhogaster*/*D. xantholophus*/*D. namaquus*
NP 390 *Dendropicos goertae*/*D. griseocephalus*
P 1 *Pitta angolensis*/*P. reichenowi*
P 5 *Mirafra passerina*/*M. cheniana*
P 6 *Mirafra rufocinnamomea*/*M. apiata*/*M. collaris*
P 7 *Mirafra africana*/*M. hypermetra* (H)
P 10 *Mirafra poecilosterna*/*M. gilletti*
P 14 *Alaemon alaudipes*/*A. hamertoni*
P 18 *Calandrella conirostris*/*C. sclateri*
P 20 *Calendrella starki*/*C. fringillaris*
P 24 *Galerida cristata*/*G. malabarica*
P 25 *Eremopterix nigriceps*/*E. signata*/*E. leucopareia*
P 26 *Eremopterix leucotis*/*E. australis*
P 31 *Hirundo nigrita*/*H. smithi*
P 32 *Hirundo lucida*/*H. aethiopica*/*H. angolensis*/*H. albigularis*
P 36 *Hirundo abyssinica*/*H. cucullata*
P 43 *Psalidoprogne obscura*/*P. pristoptera*
P 46 *Anthus pallidiventris*/*A. leucophrys* or *A. vaalensis*
P 48 *Anthus lineiventris*/*A. crenatus*
P 53 *Macronyx croceus*/*M. fulleborni*/*M. capensis*
P 54 *Macronyx ameliae*/*M. aurantigula*
P 61 *Campephaga petiti*/*C. flava* (H)
P 65 *Pycnonotus barbatus*/*P. nigricans*/*P. capensis*
P 76 *Chlorocichla falkensteini*/*C. flaviventris*
P 84 *Phyllastrephus scandens*/*P. fischeri*/*P. fulviventris*
P 95 *Prionops caniceps*/*P. rufiventris*
P 101 *Tchagra tchagra*/*T. australis*/*T. jamesi*
P 106 *Laniarius barbarus*/*L. erythrogaster*
P 107 *Laniarius turatii*/*L. aethiopicus*/*L. bicolor*/*L. ferrugineus*
P 115 *Lanius gubernator*/*L. souzae*
P 116 *Lanius excubitorius*/*L. cabanisi*
P 117 *Lanius excubitor*/*L. somalicus*/*L. dorsalis*
P 118 *Corvinella corvina*/*C. melanoleuca*
P 120 *Oenanthe bottae*/*O. pileata*
P 126 *Cercomela familiaris*/*C. scotocerca*/*C. melanura*
P 129 *Monticola brevipes*/*M. explorator*/*M. angolensis*
P 130 *Myrmecocichla aethiops*/*M. nigra*/*M. formicivora*
P 138 *Cercotrichas barbata*/*C. quadrivirgata*/*C. signata*
P 139 *Cichladusa arquata*/*C. guttata*
P 150 *Cossypha natalensis*/*C. dichroa*
P 155 *Neocossyphus finschi*/*N. fraseri*
P 157 *Turdus pelios*/*T. tephronotus*/*T. libonyanus*
P 173 *Turdoides reinwardti*/*T. tenebrosus*/*T. sharpei*/*T. hypoleucus*/*T. leucopygius*/*T. melanops*/*T. bicolor*
P 174 *Turdoides plebejus*/*T. jardinei*/*T. gymnogenys*
P 198 *Cisticola ruficeps*/*C. nana*
P 201 *Cisticola lateralis*/*C. woosnami*/*C. bulliens*
P 205 *Prinia subflava*/*P. somalica*/*P. flavicans*/*P. maculosa*
P 209 *Spiloptila clamans*/*S. rufifrons*
P 226 *Camaroptera brachyura*/*C. brevicauda* (H)
P 227 *Camaroptera simplex*/*C. stierlingi*/*C. fasciolata*/*C. subcinnamomea*
P 231 *Eremomela icteropygialis*/*E. salvadorii*/*E. flavocrissalis*
P 232 *Eremomela pusilla*/*E. canescens*/*E. scotops*
P 233 *Eremomela atricollis*/*E. usticollis*
P 240 *Macrosphenus kempi*/*M. flavicans*
P 250 *Melaenornis edolioides*/*M. pammelaina*
P 261 *Batis senegalensis*/*B. orientalis*/*B. perkeo*/*B. molitor*/*B. soror*/*B. pririt*
P 268 *Eramornis longicauda*/*E. albicauda*
P 269 *Trochocercus albiventris*/*T. albonotatus*
P 273 *Parus griseiventris*/*P. afer*
P 274 *Parus leucomelas*/*P. niger*
P 277 *Anthoscopus punctifrons*/*A. parvulus*/*A. musculus*/*A. caroli*/*A. minutus*
P 280 *Promerops cafer*/*P. gurneyi*
P 281 *Anthreptes collaris*/*A. platurus*/*A. metallicus*
P 288 *Nectarinia osea*/*N. bouvieri*/*N. habessinica*/*N. oustaleti*/*N. talatala*
P 292 *Nectarinia pulchella*/*N. chalybea*/*N. neergardi*
P 300 *Nectarinia olivacea*/*N. violacea*
P 301 *Nectarinia senegalensis*/*N. hunteri*
P 303 *Nectarinia verticalis*/*N. bannermani*
P 306 *Zosterops senegalensis*/*Z. pallida*

P 319 *Serinus mozambicus*/*S. dorsostriatus*
P 320 *Serinus leucopygius*/*S. atrogularis*/*S. citrinipectus*
P 321 *Serinus donaldsoni*/*S. sulphuratus*/*S. flaviventris*
P 330 *Ploceus melanocephalus*/*P. taeniopterus*
P 332 *Ploceus badius*/*P. rubiginosus*
P 345 *Malimbus scutatus*/*M. cassini*
P 346 *Malimbus ibadanensis*/*M. erythrogaster*
P 351 *Euplectes franciscanus*/*E. orix*/*E. nigroventris*
P 353 *Euplectes afer*/*E. diadematus*
P 361 *Passer griseus*/*P. gongonensis*/*P. suahelicus*/*P. diffusus*
P 365 *Passer luteus*/*P. eminibey*
P 366 *Petronia dentata*/*P. pyrgita*/*P. superciliaris*
P 371 *Bubalornis albirostris*/*B. niger*
P 377 *Pytilia hypogrammica*/*P. phoenicoptera*/*P. afra*
P 378 *Vidua interjecta*/*V. paradisea*
P 391 *Uraeginthus bengalus*/*U. angolensis*
P 394 *Estrilda troglodytes*/*E. astrild*
P 397 *Estrilda erythronotus*/*E. charmosyna*
P 403 *Ortygospiza atricollis*/*O. gabonensis*
P 406 *Amadina fasciata*/*A. erythrocephala*
P 409 *Lamprotornis chloropterus*/*L. acuticaudus*
P 410 *Lamprotornis caudatus*/*L. purpuropterus*
P 422 *Cosmopsarus regius*/*C. unicolor*
P 430 *Oriolus percivali*/*O. larvatus* (H)
P 436 *Corvus albus*/*C. edithae*

Neotropical Region

Amazonia

5,10 *Psophia crepitans*/*P. leucoptera*/*P. viridis*
3,12 *Ortalis guttata*/*O. motmot*/*O. supercilaris*
12 *Crax alector*/*C. globulosa*/*C. fasciolata*
9,12 *Mitu tomentosa*/*M. salvini*/*M. mitu*
10 *Pyrrhura rhodogaster*/*P. perlata*
10 *Pyrrhura melanura*/*P. picta*
10 *Brotogeris cyanoptera*/*B. chrysopterus*
8,14 *Pionites melanocephalus*/*P. leucogaster*
4 *Pionopsitta barrabandi*/*P. vulturina*/*P. caica*
7 *Neomorphus geoffroyi*/*M. pucherani*
5 *Galbalcyrhynchus leucotis*/*G. purusianus*
5 *Galbula albirostris*/*G. cyanicollis*
5 *Galbula tombacea*/*G. cyanescens*/*G. galbula*/*G. rufoviridis*
11 *Monasa nigrifrons*/*M. atra*
11 *Monasa morphoeus*/*M. atra*
10 *Malacoptila fusca*/*M. semicincta*
5 *Selenidera culik*/*S. nattereri*/*S. reinwardtii*/*S. gouldii*
5 *Pteroglossus flavirostris*/*P. bitorquatus*
5 *Pteroglossus pluricinctus*/*P. beauharnaesii*/*P. aracari*
5 *Celeus grammicus*/*C. undatus*
Hylexetastes stresemanni/*H. perrotii*
11 *Campylorhamphus trochilirostris*/*C. procurvoides* (0)
10 *Thamnophilus cryptoleucus*/*C. nigrocinereus*
9 *Cercomacra nigrescens*/*C. tyrannina*
10 *Hypocnemoides maculicauda*/*H. melanopogon*
10 *Myrmeciza melanoceps*/*M. goeldii*
10 *Thamnomanes schistogynus*/*T. caesius*
5,13 *Cotinga maynana*/*C. cotinga*
4,13 *Xipholena punicea*/*X. lamellipennis*
4,13 *Phoenicircus nigricollis*/*P. carnifex*
4 *Pipra erythrocephala*/*P. chloromeros*/*P. rubrocapilla*
4 *Pipra coronata*/*P. nattereri*/*P. vilasboasi*/*P. iris*
4 *Pipra filicauda*/*P. fasciicauda*/*P. aureola*
Lophotriccus vitiosus/*L. eulophotes*
4,15 *Euphonia rufiventris*/*E. cayennensis*
6,15 *Euphonia laniirostris*/*E. violacea* (O)
8,15 *Lanius fulvus*/*L. versicolor*
10,15 *Tachyphonus rufiventer*/*T. cristatus*

Eastern Colombia—southern Venezuela (upper Rio Negro—Rio Orinoco region)

3,12 *Ortalis guttata*/*O. motmot*
10 *Pyrrhura melanura*/*P. picta*
10 *Brotogeris cyanoptera*/*B. chrysopterus*
4 *Pionopsitta barrabandi*/*P. caica*
5 *Galbula tombacea*/*G. galbula*
11 *Monasa morphoeus*/*M. atra*
5 *Selenidera nattereri*/*S. culik*
5 *Pteroglossus pluricinctus*/*P. aracari*
10 *Veniliornis affinis*/*V. cassini*
5 *Celeus grammicus*/*C. undatus*
Xiphorhynchus ocellatus/*X. pardalotus*

Myrmotherula hauxwelli/
M. guttata
6 *Gymnopithys leucaspis*/*G. rufigula*
Tyranneutes stolzmanni/
T. virescens
6 *Cyanocorax violaceus*/*C. cayanus*
4,15 *Euphonia rufiventris*/
E. cayennensis
6,15 *Euphonia laniirostris*/*E. violacea*

NW Colombia—E Panama

6 *Aramides wolfi*/*A. cajanea*
2,6,12 *Crax rubra*/*C. alberti*
4 *Pionopsitta pulchra*/*P. haematotis*
6 *Trogon comptus*/*T. melanurus*
5,6 *Ramphastos brevis*/*R. vitellinus*
citreolaemus/*R. sulfuratus*
6 *Formicarius nigricapillus*/*F. analis*
6 *Pittasoma rufopileatum*/*P. michleri*
1,4,6 *Pipra mentalis*/*P. erythrocephala*
1,6 *Rhynchocephalus brevirostris*/
R. olivaceus
6 *Campylorhynchus albobrunneus*/
C. zonatus
6 *Psarocolius cassini*/*P. guatimozinus*
15 *Tangara lavinia*/*T. gyrola*
6,15 *Cyanerpes caeruleus*/*C. lucidus*
6,15 *Heterospingus xanthopygius*/
H. rubrifrons

Central America

Phloeoceastes guatemalensis/
P. melanoleucus
Dysithamnus puncticeps/
D. striaticeps
Synallaxis erythrothorax/
S. brachyura
15 *Lanio aurantius*/*L. leucothorax*
15 *Ramphocelus passerinii*/
R. flammigerus
15 *Thraupis abbas*/*T. palmarum*
15 *Euphonia affinis*/*E. luteicapilla*

Australia

Turnix varia/*T. olivii*
Petrophassa albipennis/*P. rufipennis*
Calyptorhynchus funereus/*C. baudinii*
Calyptorhynchus magnificus/*C. lathami*
Cacatua sanguinea/*C. pastinator*/
C. tenuirostris
Cacatua leadbeateri/*C. galerita*
Glossopsitta porphyrocephala/*G. pusilla*
Polytelis swainsonii/*P. anthopeplus*
Barnardius zonarius/*B. barnardi*
Menura alberti/*M. novaehollandiae*
Psophodes cristatus/*P. occidentalis*
Cinclosoma punctatum/*C. castanotum*/
C. alisteri/*C. cinnamomeum*
Malurus elegans/*M. pulcherrimus*/
M. lamberti
Sericornis cautus/*S. pyrrhopygius*
Sericornis beccarii/*S. magnirostris*
Acanthiza pusilla/*A. apicalis*
Acanthogenys rufogularis/*A. chrysoptera*
Lichenostomus fuscus/*L. flavescens*
Melithreptus albogularis/*M. lunatus*
Ramsayornis modestus/*R. fasciatus*
Pardalotus punctatus/*P. xanthopygius*
Poephila acuticauda/*P. cincta*
Chlamydochera maculata/*C. nuchalis*
Cracticus torquatus/*C. mentalis*

Display of the Golden-winged Manakin *Masius chrysopterus*

by D. W. Snow & B. K. Snow

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In July 1988, during a 6-week visit to La Planada, a forest reserve and biological research station in southwestern Colombia near the border with Ecuador, we spent 22 hours studying the courtship display and associated behaviour of the Golden-winged Manakin *Masius chrysopterus*, a species confined to humid subtropical forest of the Andes from western Venezuela to Peru. At the time we thought that nothing was known of its courtship; but on our return we found in our mail a recently published paper by Prum & Johnson (1987) on the Golden-winged Manakin in Ecuador, in which most aspects of the display were described in considerable detail. However, in their 164 hours of observation of territorial males Prum &